Relationship between placental surface area and fetal growth rate in artiodactyls and perissodactyls

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Short Note

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Abstract: Gestation periods in mammals are generally in line with scaling laws. There are several exceptions in which species of relatively similar size and degree of neonatal maturation show a significant difference in gestation length. For example the giraffids have a very long gestation period, compared to bovids of similar size. By using published data about the placental surface area at term, we show that in ungulates this surface area is more tightly correlated to the average fetal growth rate than to fetal and placenta weight. These data suggest that, within one type of placenta, gestation length and placental surface area are associated parameters.

Keywords: gestation period; placenta; pregnancy.

Variations in life history parameters in mammals can often not be satisfyingly explained by body size. For example, gestation periods of similar-sized animals whose neonates do not display major differences in the degree of maturity may differ distinctively, such as about 280 days in cattle (*Bos taurus*), 340 days in horses (*Equus caballus*), 390 days in the dromedary (*Camelus dromedarius*) or 440 days in the okapi (*Okapia johnstoni*) (Clauss et al. 2014). Findings on differences in gestation periods and neonate body mass thus indicate differences in intrauterine growth rates between species (Müller et al. 2011). In the search for correlates to such differences, the morphology of the placenta is an evident candidate. Across a sample of 106 mammal species, the degree of interdigitation of the placenta explained the variation in gestation periods and thus fetal growth rates (Capellini et al. 2011). Evidently, as the site of nutrient transfer from mother to fetus, the magnitude of the area available for this transfer might be one (of many) factors influencing intrauterine growth rate.

Baur (1973) presented a stereological method that facilitates in calculating this exchange area from histological and macroscopic measurements. Based on comparative measurements in 30 species, he demonstrated a fundamental difference in the full-term placental exchange area (in relation to the mass of the neonate and the placenta) between diffuse placenta types (such as found in equids, camelids, suids or hippopotamus, for example) and compact placenta types (such as found in most ruminants, primates, rodents or carnivores, for example) (Baur 1977). To our knowledge, this represents the only large scale comparative study on the placental exchange area to date.

We read the data on the placental exchange area (in m^2) and on the full-term mass of neonate and placenta (in kg) for ruminants (European domestic cow and Dwarf zebu *Bos taurus*, Giraffe *Giraffa camelopardalis*), camelids (Llama *Lama glama*, Bactrian camel *Camelus bactrianus*), suids (European domestic pig *Sus scrofa*), hippos (Dwarf hippopotamus *Choeropsis liberiensis*, Hippopotamus *Hippopotamus amphibius*), equids (Horse (thoroughbred) and Pony *Equus caballus*, Sardinian dwarf donkey *Equus asinus*, Somalian wild ass *Equus africanus*, Grant's zebra *Equus quagga*) and rhinoceros (*Rhinoceros unicornis*) from fig. 37 in Baur (1977), and added data on the gestation period for the species (Jones et al. 2009), in order to calculate the average daily growth of neonate and placenta (i.e. dividing the full-term mass by the gestation period in days). We plotted the relationships of placenta surface area to the neonatal and placental mass or growth rate for compact and diffuse placentas (Figure 1). In both cases, the relationship between neonate and placenta mass and

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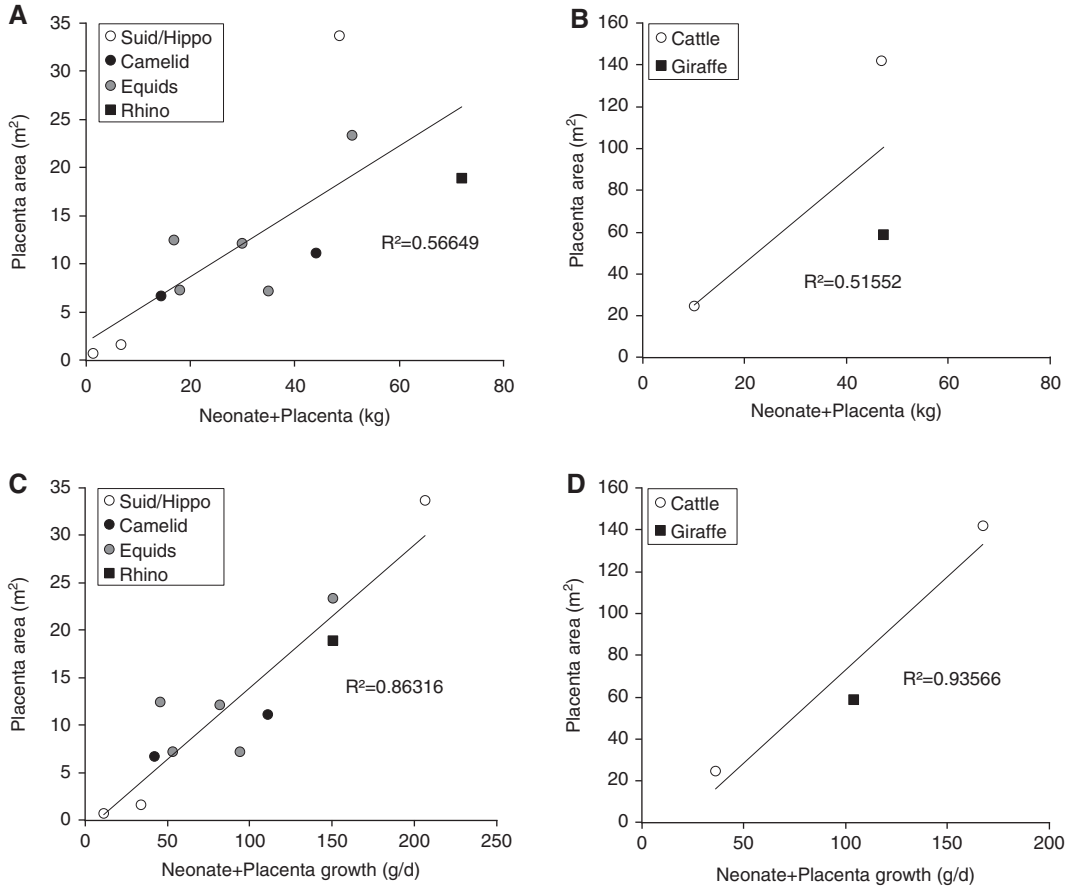

Figure 1: Relationship between the placental surface area and the mass of the full-term neonate and placenta (A, B) and the average growth rate of the full-term neonate and placenta (C, D) in artiodactyls and perissodactyls with a diffuse (A, C) and a compact (B, D) placenta. Note the generally better correlation when correlating with growth rate, i.e. taking differences in the gestation period into account, but also note the difference in magnitude of placenta area at similar growth rates between the placenta types.

placenta exchange area showed a lower correlation coefficient (Figure 1A and B) than the corresponding correlation with growth rate (Figure 1C and D). Evidently, the comparative database is far too small to allow anything but hypothesis generation.

On the one hand, the finding is that in both groups (compact and diffuse placentas), the placental exchange surface might contribute to the differences in fetal growth rates in a relevant way. This finding is in line with a general concept that nutrient and energy delivery rates, as determined by morphology, are important pacesetters for physiology and life history (West et al. 1997). On the other hand, the fundamental differences between the placenta types in the relationship of placenta exchange area and growth rate are remarkable, with animals with diffuse placentas achieving about four times the growth rate per placenta exchange area. How this is achieved – and whether the difference in morphology might represent a physiological advantage in terms of a cost saving mechanism for animals with compact placentas – remains to be elucidated. One interesting aspect is that the compact placenta of the higher ruminants evolved from a diffuse placenta, which is a stem species pattern in cetartiodactyls (Klisch and Mess 2007).

Differences in the placental exchange area within one type of placenta (i.e. diffuse or compact) thus might explain differences in the gestation period. Within the ruminants, the giraffids have exceptionally long gestation periods (Müller et al. 2011). This is linked to a relatively small placental surface area in giraffes (59 m^2, compared to 142 m^2 in the cow). Within the perissodactyls, the long gestation periods of rhinos (479 days), compared to horses (339 days), is longer than expected from their body size difference alone. This is associated with a slightly lower placental surface in the rhino (19.9 m^2), compared to the horse (23.4 m^2). The common hippopotamus has a relatively short gestation period (235 days), compared to the horse (339 days), which has similar-sized neonates. This could be

partially explained by the relatively high placental surface area of the hippo (34 m^2) compared to the horse (23 m^2).

Differences in placental exchange area, however, cannot explain the difference in gestation period between equids and camelids, which both have a diffuse placenta. Clearly additional factors must be at play. Given the more detailed investigations on the development of the placental exchange area over the gestation period in Baur (1977), which also indicate a faster increase in this exchange area in cattle than in horses, not only morphological adaptations but also the rate at which they are developed or changed may influence the magnitude of end measurements such as gestation period or neonate mass. Whether there is a difference in the rate at which a higher surface area is attained between diffuse and compact placentas, or whether more efficient nutrient transfer mechanisms that are unrelated to surface area itself are involved, remains to be investigated.

In summary, these data show that the placental surface area of artiodactyls and perissodactyls at term is more closely correlated to the average fetal growth rate than to fetal weight. These data suggest that species achieved changes of intrauterine growth rates by the evolution of different placental morphology.

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